Morphology and Relationships of
Saurocephalid Fishes

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INTRODUCTION

The few teleostean fishes known from deposits earlier than the Late Cretaceous may be referred broadly to elopomorph or clupeomorph groups. During the Late Cretaceous, a large number of different kinds of teleosteans appeared and many of these survived into the Cenozoic. Others, although occurring commonly in many deposits and inhabiting geographically widespread areas, became extinct by the end of the Cretaceous. The Saurocephalidae are one such group. Although never taxonomically diversified, they are represented in several Upper Cretaceous formations of North America, England, and Europe. Saurocephalids are most abundant in North America. This family appears to be most closely related to the ichthyodectids, which also were widely distributed geographically during the Late Cretaceous.

Saurocephalids are marine fishes reaching four feet in length. Their most striking characteristic, and one which still defies a thoroughly satisfactory explanation of its functional significance, is the unpaired, edentulous predentary bone. Although a predentary bone occurs in other teleosteans, the form of this structure in the sauro-

phalids and its relationship to the mandibles is unique among teleostean fishes.

The first species included in this family, *Saurocephalus lanciformis* Harlan, was described in 1824. The single specimen on which this name was based had been collected by Lewis and Clark in their journey up the Missouri River in 1804. This was the first vertebrate fossil to be described from west of the Allegheny Mountains. The actual locality where the specimen was found is uncertain. Evidence presented by Simpson (1942) would suggest western Iowa or eastern Nebraska. However, no similar material has been found in these areas in subsequent years. Harlan (1824) believed that this fossil, a partial maxillary, belonged among the ichthyosaurs. A second species and genus, *Saurodon leanus* Hays, (1830) was named shortly thereafter for a pair of upper and lower jaws from the Upper Cretaceous of New Jersey. During the succeeding 50 years, a host of teeth and vertebral fragments found in Europe were described and referred to these two genera. But Leidy (1857) and Woodward (1901) showed that most of the European fossils belonged to different genera and families.

The family to which the fossils discussed in this paper belong was termed Saurodontidae by Stewart (1899) and Saurocephalidae by Berg (1940). Because the generic name *Saurocephalus* has priority, the family should be called Saurocephalidae.

Abbreviations used for museum collections are:

AMNH	American Museum of Natural History
FH	Fort Hays State College Museum, Hays, Kansas
FM	Field Museum of Natural History
KU	Museum of Natural History, University of Kansas
MCZ	Museum of Comparative Zoology, Harvard University
USNM	United States National Museum
UT	University of Texas, Bureau of Economic Geology
YPM	Peabody Museum, Yale University

SYSTEMATIC DESCRIPTIONS

Infraclass Teleostei Romer, 1966

Order Ichthyodectiformes n.

Family Saurocephalidae Berg, 1940

Diagnosis.—Elongate, slender, shallow-bodied fishes.   Head contained about six times in standard length.   Preorbital part of neurocranium longer than orbital part.   Supraoccipital, with prominent crest, separated from frontals by conjoined parietals.   Epiotic with large posterior crest.   Prominent post-temporal fossa, hyomandibular fossa and subtemporal fossa.   Parethmoid anteroposteriorly elongate with large flat facet for palatine directed anteriorly.   Palatine with large hammer-like head.   Gape of mouth directed slightly upward.   Articulation of lower jaw below anterior end of orbit. Anterior end of lower jaw projects beyond upper jaw.   Premaxillary and maxillary border upper jaw.   Single, triangular, edentulous predentary articulates with mandibles.   Single row of laterally compressed teeth on all jaws.   Teeth implanted in sockets.   Vertebrae well-ossified: up to 100 centra.   First hypural expanded posteriorly; remaining 5–6 hypurals narrow, elongate.   Pectoral fin with bladelike, undivided anterior ray.

Geologic range.—Upper Cretaceous.

Saurocephalus Harlan, 1824

Saurocephalus, Harlan, 1824, p. 337.

Type-species.—*Saurocephalus lanciformis* Harlan, 1824, p. 337.

Geologic and geographic distribution.—Upper Cretaceous, United States and Europe.

Diagnosis.—Distinguished from *Saurodon* by the approximately equilateral triangular shape of predentary.   Posterior face of predentary and anterior face of dentaries with two pairs of raised articular facets which are arranged one above the other.   Irregular series of short prongs and shallow grooves on anteromedial surface of dentary interdigitate with corresponding structures on opposite dentary.   Replacement teeth enter jaws through foramina which do not open onto jaw margin.   Articular head of palatine not as thick as in *Saurodon;* lateral surface of palatine head concave.   Maxillary facet of palatine head concave; parethmoid facet flat and about one-half the length of the maxillary facet.

Saurocephalus lanciformis Harlan, 1824.   Figure 1.

Saurocephalus lanciformis Harlan, 1824, p. 337, pl. 12 (for a complete list of references to this species see Hay, 1903).

Saurocephalus arapahovius Cope, 1872, p. 343 (for a complete list of references to this species see Hay, 1903).

Saurocephalus dentatus Stewart, 1898, p. 25, pl. 1, figs. 3,4; Stewart, 1900, p. 323.

Saurocephalus pamphagus Hay, 1899, p. 303, fig. 5.

Holotype.—Incomplete maxillary.   Upper Cretaceous, near Soldier's Creek, a tributary of the Missouri River in Iowa (Simpson, 1942), Philadelphia Academy of Natural Sciences, 5516.

Geologic occurrence and distribution.—(See list of material examined for specific localities.) Niobrara Fm., Kansas, Selma Chalk, Alabama; Navesink Fm., New Jersey; Pierre Shale, South Dakota, Wyoming.

Diagnosis.—Same as for genus.

Material examined.—Approximately two dozen specimens can be definitely assigned to *Saurocephalus lanciformis*.   The better material is cited below:

Niobrara Formation (Smoky Hill Chalk member)

AMNH   7355 Butte Creek, Logan Co., Kan., maxillary, quadrate, and fragments; AMNH   7373, same loc., lower jaws; FM UF 902 Willow Canyon, 10 miles SW Russell Springs, Logan Co., Kan., incomplete neurocranium, parts of jaws; KU   109, western Kansas, mandibles; KU   154, Wallace Co., Kansas, upper jaw, predentary; MCZ   uncatalogued, Kansas, neurocranium, jaws, vertebrae.

Selma Chalk

FM PF   3557, T. 11, W of Highway 13, Hale Co., Alabama, mandible; FM P   27505, Moore Ranch, about 2 miles SE Harrell Station, Dallas Co., Ala., partial neurocranium, incomplete jaws; FM P   27509, loc. as above, Dallas Co., Alabama, parts of neurocranium and jaws.

Pierre Shale (Sharon Springs member)

FM PF   1579, 8 miles, S. Fairburn, Custer Co., S. Dakota, predentary.

Navesink Formation
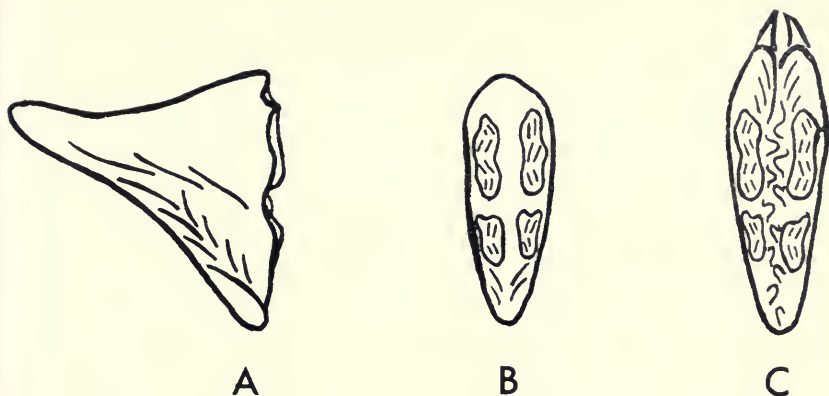
YPM   1568, 2 miles N. Mullica Hill, New Jersey, jaws.

Fɪɢ. 1.   *Saurocephalus lanciformis* Harlan.   A, Lateral view of predentary, × 1.5.   B, Posterior view of predentary, × 1.5.   C, Symphysial view of conjoined mandibles, × 1.5.   Based on uncatalogued specimen in MCZ.

Description.—About one-quarter of the total museum collections of Cretaceous saurocephalids pertain to *Saurocephalus lanciformis*. Material which permits description consists primarily of jaw elements.   No body is preserved and no neurocrania associated with *Saurocephalus lanciformis* jaws are well-preserved.

The premaxillary is somewhat higher than long and essentially trapezoidal in outline.   Length of the alveolar border ranges from 1.6–4.0 cm. (av. = 3.1 cm. for 5 specimens).   Diagonal height of the premaxillary from anteroventral to posterodorsal corner ranges from 2.8–6.3 cm. (av. = 4.9 cm. for 5 specimens).   The ratio between premaxillary alveolar border length and diagonal height of the premaxillary varies from .57–.77.   Eight to 12 alveoli are present and usually all of the alveoli are occupied by teeth.   In the two cases in which right and left premaxillaries of one individual are preserved, there are, in the first, eight alveoli in the right bone and 10 in the left (FM UF 902) and, in the second, 12 in the right and 11 in the left (USNM 3577).   Premaxillary teeth are laterally compressed with sharp anterior and posterior edges.   Only the upper part of the crowns, namely, the part where the crown begins to taper toward the acuminate tip of the tooth, projects beyond the jaw margin.   This may, however, be the result of the preservation only of the crowns of young teeth, the mature teeth having broken off at the jaw margin after death.   Foramina through which replacement teeth enter the alveoli lie about 0.5 cm. above the tooth margin. The number of foramina is equal to the number of alveoli.

The maxillary has the same shape as in *Saurodon*. Mean height of the maxillary palatine condyle from the anterior end of the maxillary dental border is 5.1 cm. (range 4–5.8 cm. for 5 specimens). Mean length of the dental border is 11.3 cm. (9.0–14 cm. for 6 specimens). The height of the maxillary relative to length of its alveolar border appears to be greater in *Saurocephalus lanciformis* than in most specimens of *Saurodon leanus* but data are inadequate for a firm conclusion about this relationship. Teeth are similar to those of the premaxillary except that more of the crown projects below the jaw margin. Twenty-seven to 38 alveoli are present with the mean about 34 for seven specimens. Tooth replacement foramina are generally 0.5 cm. above the alveolar margin. In some specimens the foramina are much closer to the alveolar border, especially posteriorly, but in no case does the foramen open into the medial margin of the alveolus.

The profile of the mandible is similar to that of *Saurodon;* variation in measurements and ratios of mandibular measurements fall within the range of *Saurodon leanus* parameters. Four entire mandibles are preserved. These range from 11.0–20.2 cm. in length from anteroventral end of the symphysis to posterior end of the dermangular (av. = 14.1 cm.). The height of the symphysis ranges from 2.1–3.3 cm. (av. = 2.6 cm. for 4 specimens). Length of the alveolar border measures 11.7 to approximately 22 cm. (av. = 15 cm. for 4 specimens). If we eliminate the largest specimen, the 22 cm. jaw (YPM 1568), the range becomes 11.7–14 cm. (av.=13 cm.). This large specimen represents the geologically youngest *Saurocephalus lanciformis* and is the only specimen from the New Jersey Cretaceous. But there seems no reason to consider this as other than an especially large individual.

Mandibular dentition is similar to that of the maxillary. Twenty-seven to 44 alveoli (av.=36 for 9 specimens) are present. The number of alveoli on the large New Jersey specimen (YPM 1568) is almost 50. A compressed, blade-like tooth occupies each alveolus. Foramina for replacement teeth lie along a groove which is a few millimeters deep. This groove lying about 0.5 cm. below the jaw margin runs the length of the alveolar border of the dentary.

On the medial surface of each dentary in the area where left and right halves meet, there is developed a series of prongs and grooves which face contrary formed structures on the dentary of the opposite side. The two mandibles interdigitate tightly by means of this peg and socket system. The anterior surface of each dentary (Fig. 1C)

shows a pair of facets arranged one above the other and each raised 1-2 mm. above the principal surface of the symphysis. These facets articulate with corresponding facets on the predentary. The upper facet when viewed from the front is dorsoventrally elongate, somewhat constricted, and its central area is slightly depressed. The facet is oval in outline and the surface is flat or slightly lower concave.

The predentary of *Saurocephalus lanciformis* (Fig. 1A and B) is easily distinguished from that of *Saurodon* by its approximately equilateral triangular shape. Five specimens measure between 2.5 and 3.0 cm. in length (av. = 2.8 cm.), and 2.5-3.3 cm. in height at the posterior end (av. = 2.7 cm.). The ratio between predentary length and height is approximately 1; while the ratio between predentary length and mandibular length ranges from .18 to .27. Dorsal and ventral borders of the predentary are somewhat concave (Fig. 1A). There may also be a concave groove on each side of the ventrolateral surface.

On the posterior surface (Fig. 1B) of the predentary there are two pairs of stout facets arranged one above the other. These facets do not touch each other. The upper facets are dorsoventrally elongate and slightly constricted midway along their length. The articular surface of this facet is bent by this constriction into a concave dorsal moiety which faces directly posteriad and a less concave lower area pointing ventroposteriad. The lower pair of facets are ovoid and essentially flat.

PALATE. The palatine (Hay, 1899, Fig. 3) is characterized by an enlarged head which articulates dorsally with the parethmoid and ventrally with the maxillary. Relative to *Saurodon,* the palatine head of *Saurocephalus lanciformis* is less swollen and its lateral surface is concave. The articular facet for the parethmoid is about one-half the length of the maxillary facet, and the former is flat while the latter is concave.

Discussion.—Each of the four nominal species of *Saurocephalus* is based on jaw elements. None shows sufficiently characteristic differences to warrant specific distinction when the set of jaw material now in museum collections is examined. *Saurocephalus arapahovius* Cope (type: AMNH 2073) is an undistinguished maxillary fragment which Hay (1903) placed in synonymy with *S. lanciformis* upon finding that the differences cited by Cope (1872) were not really present.

Saurocephalus dentatus Stewart (type: KU 154, old no. 82) was established for an upper and lower jaw which Stewart distinguished from *S. arapahovius* by (1) the slight striation of the teeth which do not overlap each other and (2) its slightly larger size. Maxillary as well as mandibular teeth of some specimens show vertical striae, perhaps 6–10 per side of the tooth. However, this character exhibits no uniform variation and does not seem to have taxonomic significance. I see no evidence for overlapping of sides of teeth on the type of *S. arapahovius*. While a few *Saurocephalus* specimens show such overlapping at some points along upper or lower jaws, this probably represents irregular, individual variation.

Saurocephalus pamphagus Hay (type: AMNH 7355) comprises a right maxillary, part of the left maxillary, both quadrates, and a palatine. Hay distinguished the maxillary of his material from *S. dentatus* by its somewhat (17%) greater length but noted that the height of the palatine condyles of both species was about the same. The number of alveoli in these two nominal species is also approximately the same: 38 in *S. dentatus*, 38–40 in *S. pamphagus*. A most important difference which Hay did not consider, however, is the condition of the maxillary. This bone was damaged or diseased during the life of the fish. An elongate swelling has thickened the posterior lower half of the maxillary. The resulting exostosis has altered the length of the bone so that the differences cited by Hay cannot be used to establish this species.

Except for the type of *Saurocephalus lanciformis*, types of the other species came from the Niobrara Fm. of Kansas. In summary, there seems no reason for recognition of more than a single species of *Saurocephalus* in North America.

The only other species definitely assignable to this genus, *Saurocephalus woodwardii* Davies (1878) comes from the Upper Cretaceous of Maastricht, Holland. Judging from the descriptions of Davies (1878) and Woodward (1901), this species is probably indistinguishable from *S. lanciformis*. The maxillary of *S. woodwardii* is incomplete. Proportions of the incompletely preserved mandible and the number of mandibular teeth are within the range of *S. lanciformis*. Woodward suggested that at least 50 mandibular alveoli were present. This is about the same number as in the New Jersey specimen which comes from an equivalent Maastrichtian horizon. In this character, the two geologically latest specimens of *Saurocephalus* are similar. Taxonomic distinction of *S. woodwardii* is retained tentatively, based on its geographic occurrence.

Saurodon Hays, 1830

Saurodon Hays, 1830, p. 475
Daptinus Cope, 1873, p. 339

Type-species.—*Saurodon leanus* Hays, 1830, p. 475.

Geologic occurrence and distribution.—Upper Cretaceous: United States, England.

Diagnosis.—Distinguished from *Saurocephalus* by the isosceles-triangle-shaped predentary, the posterior face of which is rhomboidal in outline. Articular facets on posterior face of predentary not well-defined; facets comprise a lateral pair and a faint dorsoventral pair. Anteromedial symphyseal surfaces of mandibles rugose but not with prongs and grooves. Replacement teeth enter alveoli through elongate grooves which usually open onto alveolar margin.

Saurodon leanus Hays, 1830.   Figures 2–8.

Saurodon leanus Hays, 1830, p. 476, pl. 16; Leidy, 1857, p. 91, pl. 6, figs. 12–15; Cope, 1877, p. 588.

Saurocephalus prognathus Cope, 1870, p. 532; Cope, 1871, p. 417.

Ichthyodectes prognathus Cope, 1872, p. 340, 343; Cope, 1872, p. 340; Cope, 1875, p. 210, 274, pl. 46, figs. 6–10; Crook, 1892, p. 123; Hay, 1898, p. 226.

Saurocephalus phlebotomus Cope, 1870, p. 530 (for a complete list of references to this species see Hay, 1903).

Daptinus phlebotomus (Cope), 1873, p. 339 (for a complete list of references to this species see Hay, 1903).

Saurodon phlebotomus (Cope), 1877, p. 588 (for a complete list of references to this species see Hay, 1903).

Daptinus phlebotonum Crook, 1892, p. 123.

Daptinus broadheadi Stewart, 1898, p. 24, pl. 2, fig. 1.

Saurodon broadheadi Stewart, 1898, p. 178.

Saurocephalus broadheadi Loomis, 1900, p. 252, pl. 24, fig. 6, pl. 25, fig. 1.

Saurodon xiphirostris Stewart, 1898, p. 178, pl. 14; Stewart, 1900, p. 314, pl. 55; Loomis, 1900, p. 247.

Saurocephalis xiphirostris Hay, 1903, p. 51.

Saurodon phlebotomus Loomis, 1900, p. 248, pl. 24, figs. 1–5.

Saurodon ferox Stewart, 1898, p. 183, p. 25, pl. 26, figs. 1–3; Stewart, 1900, p. 319, pl. 56, pl. 57, figs. 1–3.

Ichthyodectes goodeanus Cope, 1877, p. 176; Hay, 1898, p. 227.

Saurocephalus goodeanus Hay, 1903, p. 52, fig. 41.

Holotype.—Upper and lower jaws. Upper Cretaceous: Navesink Marl, Pennsauken Creek, 5 miles SE of Moorestown, New Jersey. Washington, D.C. USNM 3577.
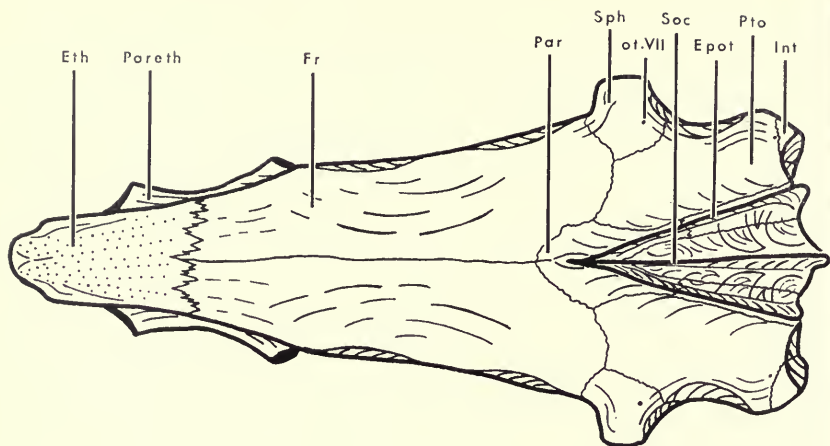
FIG. 2. *Saurodon leanus* Hays. Dorsal view of neurocranium, × 1.5.

Geologic occurrence and distribution.—(See list of material examined for specific localities.)   Austin Chalk, Texas; Niobrara Fm., Kansas; Selma Chalk, Alabama; Pierre Shale, Wyoming, South Dakota; Navesink Fm., New Jersey; Vermilion River Fm., Manitoba.

Diagnosis.—Same as for genus.

Material examined.—Approximately 100 specimens referable to *Saurodon leanus* were seen.   The great majority of this material includes those structures which permit certain generic identification. However, some specimens including a few neurocrania lacking associated jaws or palate are sufficiently similar to definitive *Saurodon leanus* material so that these are included in this list.   The better preserved material and specimens from several geographic localities are cited below:

Austin Chalk

UT acc. no. 91–90, Wallace Quarry, Grayson Co., Texas, parts of head and vertebral column; UT uncatalogued, Savoy Quarry, Fannin Co., Texas, incomplete jaws and other fragments.

Niobrara Fm. (Smoky Hill Chalk member)

YPM 3942, Butte Creek, Logan Co., Kansas, neurocranium; MCZ 5342, Trego Co., Kan., jaws; FM UC 1333, Gove Co., Kan., head; FM PF 3337, R. 35 W, T, 15 S, sec. 11, SE¼, Logan Co., Kan., head, vert., fins; FM PF 3741, R. 35 W, T. 15 S, sec. 11, SE¼, Logan Co., Kan., complete fish; FH 11322, R. 35 W, W. 15 S, (Cedar Canyon), Logan Co., Kan., head and vertebral column;

KU 142, Spencer's Canyon, R. 25 W, T. 14 S, Gove Co., Kan., quadrate and mandibles; KU 155, Wallace Co., Kan., maxillary and dentary; KU 153, Wallace Co., Kan., maxillary and predentary; KU 343, western Kan., head; KU 464, Trego Co., Kan., jaws; AMNH 2110, Gove Co., Kan., jaws and palatine; AMNH 1907, R. 19 W, T. 4 S, Phillips Co., Kan., premaxillary; AMNH, 1648, western Kan., head; AMNH 7354, Butte Creek, Logan Co., Kan., neurocranium and jaws; AMNH 8323, Elkader, Logan Co., Kan., pectoral girdle; AMNH 8544, Hell Creek, R. 31 W, T. 15 S, Gove C., Kan., neurocranium, jaws, vertebrae.

Vermilion River Fm.

?FM PF 5407, R. 27 W, T. 39 N, sec. 2, S½, Manitoba Canada, vertebrae.

Selma Chalk

FM P27508, Moore Ranch, about 2 miles SE, Harrell Station, Dallas Co., Alabama, mandible and predentary; FM PF 122, 1.6 miles NW Greene, Greene Co., Ala., incomplete mandible; FM P27413, Moore Ranch, about 2 miles SE Harrell Station, Dallas Co., Ala., mandible; FM P27530, same locality as above, upper and lower jaws and head fragments; FM P27435, same locality as above, parts of upper and lower jaws; FM PF 123, .5 miles N, Mt. Hebron, Dallas Co., Ala., rear of neurocranium and jaws; FM P27483, Moore Ranch, about 2 miles, SE, Harrell Sta., Dallas Co., Ala., part of neurocranium, jaws, palate, vertebrae.

Pierre Shale

Several uncatalogued specimens at AMNH.

BODY.   Only one specimen, FM PF 3741 (standard length about 130 cm.) shows an entire vertebral column including head and tail. The head of this fish is contained approximately six times in the standard length.   The ribs are not completely preserved.   However, judging from (1) the size of and positions of the preserved rib fragments, (2) partial skeletons showing complete ribs and (3) comparison with the closely related ichthyodectids, *Saurocephalus leanus* was an elongate, narrow-bodied, slender fish.

NEUROCRANIUM.   Thirteen intact, complete neurocrania are preserved but all are compressed laterally or dorsoventrally.   The narrow, elongate preorbital ends of neurocrania are more commonly preserved.

In dorsal view (Fig. 2) the neurocranium resembles an isosceles triangle. Mean neurocranial length is about 16.4 cm. (range 12.1– 22.0 cm., Table 1) measured from anterior end of the ethmoid to posterior end of the epiotic. Three thin ridges of bone arise from the dorsoposterior surface of the neurocranium. These are a pair of lateral ridges formed of parietal and epiotic and a medial ridge produced by the parietal and supraoccipital. The lateral ridges are directed anteromedially and intersect the central ridge above the posterior border of the orbit. Elongate anteriorly tapering areas between the crests were occupied in life by epaxial musculature. A lateral projection formed by the sphenotic arises three-quarters of the way between anterior and posterior ends of the neurocranium.

In lateral aspect (Fig. 3) the neurocranium exhibits a straight dorsal line except at the extreme anterior end where the front of the ethmoid is bent slightly ventrad and at the posterior end where the supraoccipital crest rises steeply toward its posterior edge. The ventral border of the neurocranium, primarily formed by the parasphenoid, is bent sharply upward anteriorly and posteriorly from the posteroventral corner of the orbit. As a result, a slender elongate preorbital or snout region is produced. The snout is approximately $1^1/_5$ times longer than the orbit. The postorbital part of the neurocranium is shorter, measuring only three-fourths of orbital length. The angle between the section of the parasphenoid lying below the orbit and snout and the section below postorbital part of the neurocranium is about 145° to judge from measurements of three specimens which show little or no distortion of the parasphenoid.

TABLE 1. Neurocranial lengths of *Saurodon leanus* measured from anterior end of the ethmoid to posterior end of the epiotic.

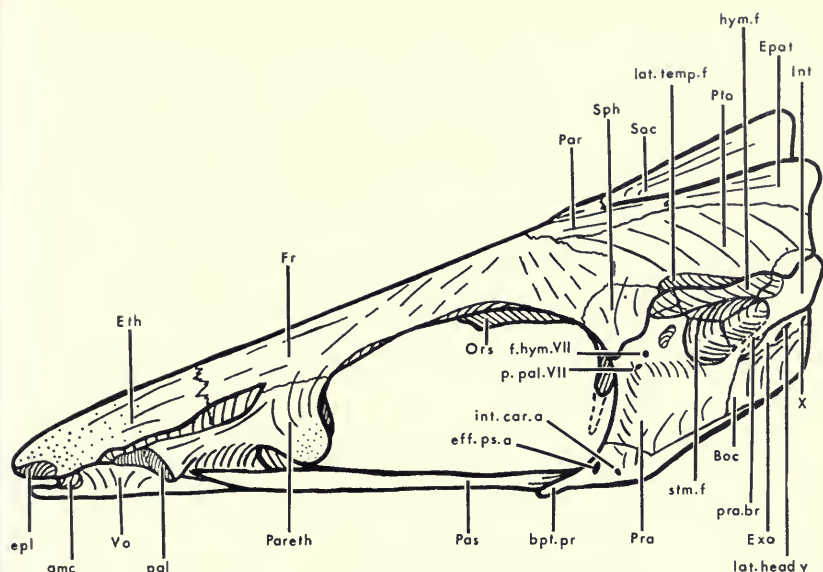| Specimen		Length
AMNH	7354	16.5 cm.
AMNH	8544	12.1
AMNH	——	20.0
FH	1990	*18.5
FH	11322	13.5
MCZ	——	14.8
KU	161	12.5
KU	162	14.5
KU	277	17.0
KU	297	19.5
KU	343	18.5
KU	12094	22.0
YPM	3942	*14.0

* Asterisk indicates approximate measurement.

FIG. 3. *Saurodon leanus* Hays. Lateral view of neurocranium, × 1.5.

The principal fossae which appear in lateral view and involve more than a single bone are:

(1) Hyomandibular fossa, an elongate dumbbell-shaped depression in the pterotic, sphenotic, prootic and intercalar.

(2) Subtemporal fossa lying below the hyomandibular fossa and involving the pterotic, prootic and exoccipital. The adductor hyomandibulae muscle originated within this depression.

(3) Nasal capsule walled by ethmoid and parethmoid.

Viewed posteriorly, the neurocranium is rhomboidal in outline with its greatest width across the intercalars. A post-temporal fossa extends anteriorly under the cranial roof and is bordered by the pterotic, intercalar, exoccipital and epiotic. A shallow, dorsoventrally elongated depression, the subepiotic fossa, lies within epiotic, supraoccipital and exoccipital. Both of these fossae served for attachment of epaxial musculature.

The ethmoid is the most anterior bone in the neurocranium. This bone meets the vomer and parethmoids ventrally and the frontals posteriorly. The position of the ethmofrontal juncture is indicated by a zigzag suture lying about half way across the nasal capsule. Many small pores, part of the sensory canal system, are

scattered across the dorsal surface of the ethmoid. Such pores are not as well developed on the frontals and this difference helps one to distinguish the division between these bones. The ethmofrontal suture if followed laterally divides the nasal capsule into anterior and posterior halves. Maximum ethmoid length measured from rostral tip to ethmofrontal suture is included about $3\frac{1}{2}$ times in total neurocranial length. Anteriorly the ethmoid ends in a narrow prong which may be slightly cleft in the median plane. Posterior to this prong the ethmoid expands laterally forming a pair of projections. A facet developed on the anterior surface of this projection and extending along the lateral surface of the anterior prong of the ethmoid was occupied by ligaments which joined premaxillaries and ethmoid.

The vomer, an elongate, slender bone, begins just posterior to the front end of the ethmoid and runs to a point below the anterior end of the orbit. Vomer and ethmoid are fused dorsally posterior to the lateral projections of the ethmoid. The vomer and parethmoids meet ventral to the nasal capsule. A pair of anterior-facing facets situated at the broadest part of the vomer directly behind the lateral ethmoid projections receive the anterodorsal condyle of the maxillary. No teeth were observed on the vomer.

The paired parethmoids join the ethmoid anteriorly, frontals dorsally, parasphenoid and vomer ventrally. Parethmoids do not appear to meet dorsally but they probably join ventrally, below the ethmoid and dorsal to the vomer to form the medial and posterior walls of the nasal capsule. The most characteristic feature of the parethmoid is the stout, elongate process which forms the ventral border of the nasal capsule and ends below the anterior border of this capsule in a stout head with a flat, transversely ovoid facet. This facet which is extended by a slender process anteromedially along the lateral surface of the snout serves as the receptacle for the enlarged head of the palatine. Parethmoids are composed of two parts; an anterior, endochondral part formed of cancellous bone and a posterior dermal part of laminar bone. The suture separating the two parts runs dorsoventrally across the posterior third of the nasal capsule. The lateral surface of the dermal portion bears minute pores. The point of emergence of the olfactory nerve is uncertain since the central area of the nasal capsule is not well preserved.

Paired frontals roof the orbit, join ethmoid and parethmoid anteriorly, sphenotics posterolaterally, pterotics and parietals posteriorly, orbitosphenoid and pterosphenoids ventrally. A pair of elon-

gate grooves above the orbit on the dorsolateral surface of the frontal indicate the positions of supraorbital and dermosphenotic circumorbital bones.   Rows of sensory canal pores appear as radiating lines extending anteriorly and laterally across the dorsal surface of the frontals.

The paired sphenotics are characterized by a stout lateral process from which the levator arcus palatini ran to the hyomandibular and metapterygoid.   The surface area for attachment of this muscle is increased by a triangular-shaped depression on the ventral surface of this process.   A foramen for the otic branch of the seventh nerve is located on the posterodorsal surface of the sphenotic.   The sphenotic is sutured to the frontal dorsally and anteriorly, pterotic dorsally and posteriorly, prootic ventrally and pterosphenoid medially.

The medially united parietals join frontals anteriorly, pterotics laterally, epiotics and supraoccipital posteriorly.   Anterior parts of the three ridges on the dorsal side of the neurocranium are formed by the parietals.   The parietal contributes one-half the length of the parietoepiotic ridge.   Toward the midsagittal line, the parietals form a low hump which constitutes the anterior end of the parieto-supraoccipital ridge.

The paired epiotics join parietals anteriorly, supraoccipital medially, pterotics laterally, and exoccipitals posteroventrally.   Medially-directed ridges run from the epiotics to unite with similar ridges on the supraoccipital and help brace the supraoccipital crest.   In posterior view, a vertical element of the epiotic forms the medial wall of the post-temporal fossa and lateral wall of the shallow subepiotic fossa.   The epiotic crest rises to approximately one-half the height of the supraoccipital crest but because distal edges of the latter are incompletely preserved, this must be considered an estimate.

The supraoccipital joins parietals anteriorly and laterally, epiotics laterally, and exoccipitals posteroventrally.   The characteristic feature of the supraoccipital is a thin sagittal crest.   This crest may (FM PF 3741) extend up to a centimeter or two beyond the posterior end of the epiotic crest.

The paired pterotics cover most of the postorbital portion of the neurocranial roof.   Pterotics meet frontals anteriorly, parietals and epiotics medially, sphenotics anterolaterally, prootics and exoccipitals ventrally, and exoccipitals and intercalars posteriorly.   Several functionally significant structures are formed in part or whole by the pterotic.   The lateral temporal fossa, a slender, half-moon-shaped

depression located on the upper surface of the pterotic just above the hyomandibular fossa, served as the principal origin of the dilatator operculi muscle. The mid-section of the hyomandibular fossa and the roof of the subtemporal fossa are formed by the pterotic. A small foramen on the dorsal surface of this bone just anterior to its suture with the intercalar carried a sensory branch of the seventh nerve.

The parasphenoid meets the vomer anteriorly, parethmoids, pro-otics, and basioccipitals dorsally. At the posteroventral corner of the orbit, the parasphenoid is bent. One side extends anterodorsally and forms the ventral border of the orbit; the other runs posterodorsally and completes the ventral border of the otic section of the neuro-cranium. At the level of the posterior end of the parethmoid, the parasphenoid bifurcates and the two arms extend anteriorly to a point below the palatine facet of the parethmoid. Below the basi-occipital, the parasphenoid again bifurcates and the arms extend almost to the posterior end of the neurocranium. Beneath the orbit, the parasphenoid is triangular in cross-section, the apex at the mid-dorsal line. Stout, anterolaterally directed prongs, the basipterygoid processes, arise from the parasphenoid at the ventroposterior corner of the orbit. Short, thin flanges of the parasphenoid extend upward about 1 cm. forming the lateral wall of the myodome canal. Two foramina lie posterior to the basipterygoid process; the anterior one probably carried the efferent pseudobranchial artery and the posterior one the internal carotid artery. The parasphenoid must be attached weakly to the other skull bones because it is not always preserved, especially on dorsoventrally crushed specimens.

The prootics occupy more than half of the lateral neurocranial wall posterior to the orbit. Each prootic meets pterosphenoid and sphenotic dorsally, basisphenoid medially, pterotics posterodorsally, parasphenoid ventrally, exoccipitals, intercalars (?) and basioccipital posteriorly. The anteroventral corner of the hyomandibular fossa is incised into the prootic and posteriorly the prootic is depressed medially forming the anterior wall of the subtemporal fossa. A narrow strut of the prootic appears to run dorsoposteriorly lateral to the ventral border of the subtemporal fossa toward a ventroan-teriorly directed projection of the intercalar. In the ichthyodectids such as *Xiphactinus*, a suture between these bones is clearly present, but on the thinner-boned *Saurodon* neurocrania, the connection might have been a thin strut of bone or cartilage.

Three foramina appear on the lateral wall of the prootic.   One foramen lying ventral to the hyomandibular fossa carried the hyomandibular branch of the seventh nerve.   The second foramen, ventral to the first, carried the posterior palatine branch of the seventh nerve and perhaps also the orbital artery.   The third foramen, the passageway for the lateral head vein, lies anterior to the basioccipital-prootic suture and just within the ventral edge of the subtemporal fossa.

The portion of the postorbital wall (Fig. 4B) formed by the prootic is poorly preserved but the principal foramina can be identified.   The largest opening is that from the trigeminofacial chamber. This opening is divided by a transverse bar of bone.   Fifth and seventh nerves, orbital artery and lateral head veins emerged through this opening.   A small foramen dorsal or in some specimens dorsomedial to the trigeminofacial foramen probably carried an accessory blood vessel or nerve.   Lateral to the basisphenoid but still within the prootic is the foramen for the oculomotor nerve.   Two foramina open through the prootic into the myodome canal.   The smaller one lies ventroposterior to the oculomotor foramen and carried the sixth nerve.   The larger foramen is ventrolateral to the oculomotor foramen and carried the palatine branch of the seventh nerve.

The orbitosphenoid is the central, anterodorsal element within the orbit.   This bone joins the frontals laterally and pterosphenoids posteriorly.   A prong of the orbitosphenoid extends to the dorsal border of the optic fenestra.   The olfactory nerve entered the orbit through a medial opening in the orbitosphenoid and a pair of foramina for anterior cerebral veins penetrate the orbitosphenoid lateral to the olfactory nerve opening.

The paired pterosphenoids form the dorsoposterior wall of the orbit.   Each pterosphenoid meets orbitosphenoid anterodorsally, frontal anterolaterally, sphenotic laterally, basisphenoid posteromedially, and prootic posteroventrally.   Pterosphenoids, basisphenoid, and part of the orbitosphenoid surround the optic fenestra.   A foramen in the pterosphenoid lying lateral to the optic fenestra probably carried secondary branches of the fifth and seventh superficial ophthalmic nerves.

The basisphenoid is a triradiate median bone.   The lateral wings are sutured to pterosphenoids and prootics.   The third wing of the basisphenoid projects ventrally and probably joined the parasphenoid by a cartilaginous extension or a very slender piece of bone which has not been preserved.
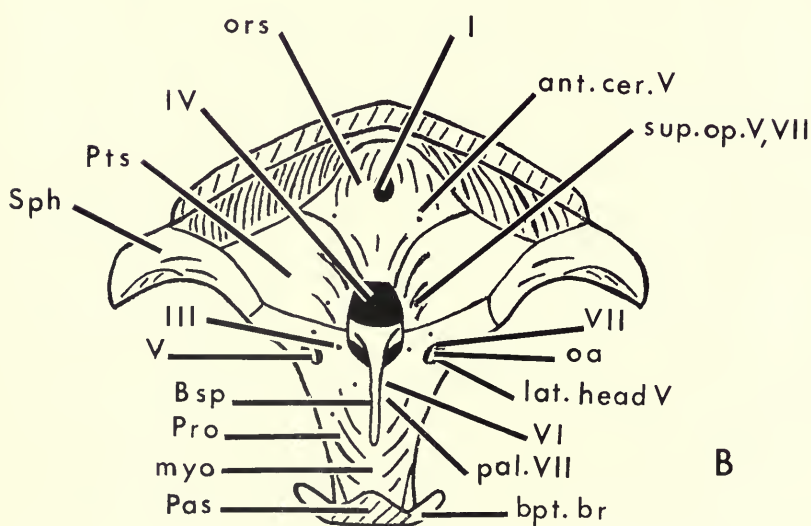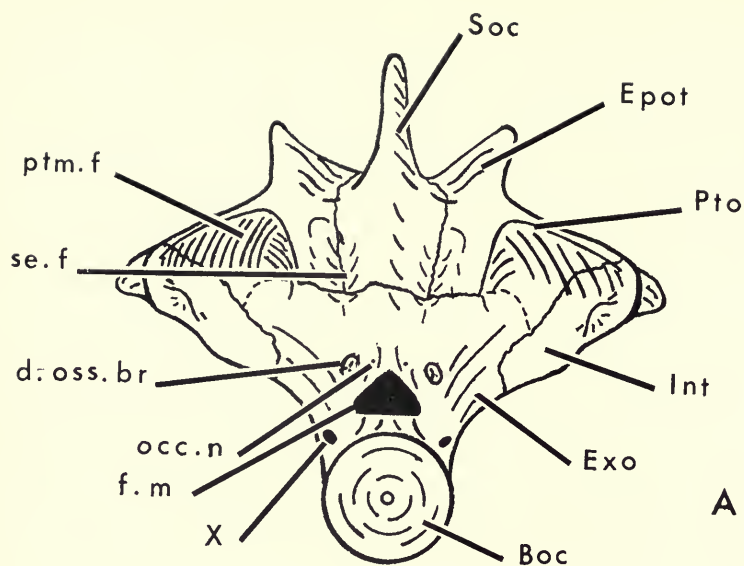
FIG. 4. *Saurodon leanus* Hays. A, Posterior view of neurocranium, × 1.5. B, Postorbital wall of neurocranium, × 1.5.

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The basioccipital forms the posteroventral corner of the neuro-cranium. It meets prootic anteriorly, parasphenoid ventrally, exoc-cipital dorsally and the first centrum posteriorly. As in *Tarpon*, an anterior projection of the swim bladder probably extended forward along the lateral concavity of the basioccipital.

The paired exoccipitals form most of the posterior surface of the neurocranium (Fig. 4A). The exoccipital meets the prootic anter-iorly within the subtemporal fossa. Laterally, intercalar, epiotic, and supraoccipital cover most of the exoccipital. Ventrally the ex-occipital joins the basioccipital, and dorsally the exoccipital is su-tured to epiotic and supraoccipital. Both exoccipitals unite to form the margins of the foramen magnum. The lateral head vein runs forward along the exoccipital and through a canal formed within the lateral portion of this bone. This canal opens anteriorly into the subtemporal fossa. The tenth nerve emerged from the neuro-cranium through a foramen just posterior to the canal for the lateral head vein. A pair of depressions in the exoccipital lateral to the foramen magnum were points of attachment of anterior intermuscu-lar bones.

The paired intercalars form the posterolateral corner of the neuro-cranium. Each intercalar joins a pterotic dorsally, and an exoccipi-tal medially and posteriorly. The posterior section of the hyoman-dibular fossa is set into the intercalar. A knob-like protuberance on the posterior surface of the intercalar received the lateral arm of the post-temporal bone.

MAXILLARY-MANDIBULAR SERIES. Entire, intact jaws and parts of the jaws are the most commonly preserved material pertaining to this species. Three or four elements comprise the upper jaw: pre-maxillary, maxillary, and one or perhaps two supramaxillaries. The lower jaw includes five bones: dentary, derm- and autangulars, retro-articular, and coronomeckelian.

In lateral view the premaxillary is approximately rhomboidal in outline (Fig. 5). Summaries of measurements of premaxillary height, length, and numbers of alveoli are given in Table 2. Anteriorly this bone is about 5-7 mm. thick, its anteromedial surface roughened to provide a firm anchorage for interpremaxillary ligaments. The ven-tral border is as thick as the anterior and slightly convex downward. Posteriorly the premaxillary border shows a slightly irregular out-line. This border tapers to a feather edge where premaxillary and maxillary join. Dorsoposteriorly the premaxillary becomes narrow and pointed. The anterodorsal edge is thickened and the medial
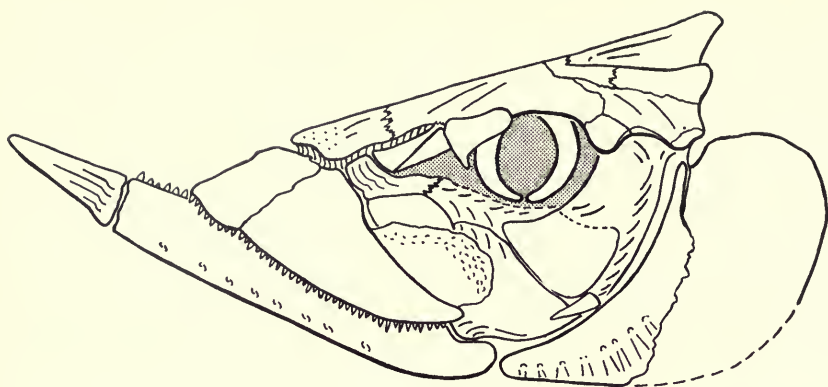
Fig. 5. *Saurodon leanus* Hays.   Head, × 0.67.   Based primarily on KU 161 and KU 343.

surface roughened for attachment of the premaxillary-ethmoid ligament.   A depression of irregular outline on the medial surface of the premaxillary received the anterior portion of the maxillary.   The lateral surface of the premaxillary is characterized by numerous little pits.   Randomly distributed ventrolaterally, these pits tend to be arranged in linear rows dorsally.   Just above the dental border, the lateral surface is thrown into irregular, low rugose folds.

Premaxillary teeth are lodged in alveoli which may extend 1–1.5 cm. into the bone.   Teeth project anteroventrally up to 6 mm. beyond the alveolar border.   Each tooth is pointed and has sharp anterior and posterior edges.   The medial border of each alveolus is interrupted by a channel which extends upward and then expands to form a round foramen about 2–4 mm. above the alveolar border. Replacement teeth entered each alveolus through these foramina. In some cases (KU 343) in the jaw of one individual, the neck of the channel leading to one or more foramina may be closed off from the alveolus by a bony bridge.

The maxillary is rather deep and short; its height measured from the posterior end of the palatine condyle to the anterior end of the dental border is contained about 1.7–2.6 times in the length of the dental border.   For summaries of other maxillary measurements and numbers of alveoli see Table 2.   The profile of the ventral border is convex except for a slightly concave part just behind the facet for the head of the palatine.   Anterior to this facet, the maxillary curves medially at about 30° to its longitudinal axis.   This curved portion

TABLE 2.   Measurements of jaw bones and numbers of
alveoli of *Saurodon leanus*.

	N	$\overline{X}$	Range
Premaxillary			
Length of dental border	17	3.8 cm.	2.2–5.5 cm.
Height (anteroventral corner to posteroventral corner)	18	5.6	3.5–7.0
Number of alveoli	16	10.5	7?–8–13
Maxillary			
Length of dental border	15	8.8	6.4–11.3
Height (post. end palatine condyle to ant. end dental border)	23	4.8	2.5–6.1
Number of alveoli	13	32	29–36
Mandible			
Length of dental border	16	12.8	8.7–16.8
Height of symphysis	22	2.6	2.0–3.3
Height at posterior end of dental border	10	4.8	3.0–5.7
Total length (anteroventral end of symphysis to post. end of angular)	13	16.0	9.5–20.5
Number of alveoli	16	41	31–54
Angle between symphysial and ventral borders	10	103°	100°–106°
Predentary			
Height at posterior end	13	2.6	2.1–3.0
Length	11	5.3	3.0–7.0

tapers in thickness anteriorly and is firmly joined to the premaxillary. A pair of articular facets is developed on the anterodorsal surface of the maxillary. The slender, short anterior facet is somewhat raised above the principal surface of this portion of the maxillary. This facet articulated with the anterior-facing facet of the vomer. The posterior maxillary facet, about three times larger than the anterior facet, reaches about 1 cm. in length and 0.5 cm. in width. These facets which must have been covered by cartilaginous capsules articulated with vomer and palatine respectively such that the maxillary could rotate forward on the divided fulcrum of its neurocranial articulation.

A series of closely-spaced alveoli is present. Nearly every alveolus is filled with a tooth. Alveoli lacking teeth appear to have lost them at or shortly before death for in few cases are the alveoli resorbed. The shape of the teeth is similar to those of the premaxillary but the crowns project ventrad rather than anteroventrad. Foramina for replacement teeth are developed as in the premaxillary.

At least one deep, short supramaxillary is attached to the maxillary behind the palatine condyle. A clear suture separating an anterior from a posterior supramaxillary cannot be discerned.

The mandible is an elongate, essentially rectangular unit (Fig. 6). Summaries of mandibular measurements and alveolar counts are given in Table 2. The symphysis is straight. Its anteromedial surface is irregularly rugose where the dentaries come into contact with each other. On the medial surface of the symphysis the larger dentaries exhibit a pair of deep depressions (FM P 27413) about 3–4 mm. in length arranged one above the other and separated by a thin lamina of bone. Small protuberances in a similar location on the opposite jaw articulate with these depressions.

The profile of the dorsal mandibular border rises gradually to the posterior end of the dental border, then slopes steeply toward the posterior hook-like projection of the dermangular. No coronoid process is developed. The ventral edge of the mandible is straight.

The lateral surface of the dentary is smooth except for scattered small punctae, probably foramina for small blood vessels. Just above the ventral border, a series of small depressions houses receptors of the mandibular sensory canal. Characteristic of the medial surface of the dentary just posterior to the symphysis and in front of the anterior end of the dermarticular is a longitudinally oriented depression whose length is about equal to symphysial height and whose depth is about one-half symphysial height. This depression, which reaches a maximum of about 0.5 cm. in depth, probably was occupied by the intermandibularis muscle.

The dental border bears a series of alveoli with nearly every one occupied by a tooth. Teeth are acuminate, compressed laterally with sharp anterior and posterior edges. Channels lead downward from each alveolus to enlarged foramina as in the upper jaws. On some specimens these channels are closed by a bridge of bone but the foramina are neither as far from the dental border as in *Saurocephalus* nor contained in a longitudinal groove. A clear pattern of tooth succession is not discernible from the size of the preserved crowns or the area of the alveolus occupied by each tooth. A pattern, if such existed, produced essentially complete occupation of the alveoli and a fully mature set of teeth at least in alternate alveoli. Replacement must have been rapid to judge from the presence of few short, incompletely exposed crowns.

The dermangular is a wedge-shaped bone extending along more than half of the medial surface of the mandible. It is bent in such

a way that a flat, elongate ledge is produced along the dorsal surface of its medial extent.   The large adductor mandibulae muscle is attached to this ledge.   A shorter part of the dermangular appears on the lateral mandibular surface and extends to the posterior end of the mandible where it forms a hook-like process.   The autangular is a shorter bone, between 1–2 cm. in length and height.   Of irregular proportions, its most characteristic feature is the slightly concave posterior surface for articulation with the quadrate.   There is a small retroarticular at the posteroventral corner of the mandible sutured to dentary, dermangular and autangular.   The irregularly-shaped, thin coronomeckelian lies in the corner formed by the dermangular and autangular anterior to the articulation of the quadrate.

The predentary has the form of an isosceles triangle (see summary of measurements of this bone in Table 2).   The ratio between predentary height and length varies from about .37–.48, which is less than half that of *Saurocephalus lanciformis*.   The ratio between predentary length and mandibular length ranges from .28–.39.   The predentary is thickest at the symphysial end and tapers anteriorly to a blunt tip which frequently is broken on the fossils.   Dorsal and ventral surfaces are rounded while the lateral surfaces are flat.   A pair of elongate, ovoid facets lies about midway along the rhomboidal, posterior face of the predentary.   A third facet is situated at the midsagittal line near the dorsal border and a fourth midsagittally near the ventral border.   These facets are much less distinct.   None of these facets is raised from the posterior surface of the predentary as in *Saurocephalus*.

HYOPALATINE BONES.   Hyopalatine elements are poorly preserved and can be examined on only a few specimens (KU 343, AMNH 1648).   The hyomandibular is curved anteriad carrying the suspensorium forward so that articulation of the lower jaw lies below the anterior end of the orbit.   At its articulation with the neurocranium, the hyomandibular has, in dorsal view, an hour-glass shape.   Below the neurocranium this bone gradually expands anteroposteriorly to the level of its broad junction with the metapterygoid.   A narrow strut of the hyomandibular extends ventrad posterior to the metapterygoid and joins the symplectic.   There does not appear to be any contact with the quadrate.   A prominent vertical ridge extends along the length of the lateral surface of the hyomandibular from just below the articulation with the neurocranium to just above the symplectic.   The preoperculum fits snugly against the posterior edge of this ridge.   An elongate, posteriorly convex facet on the posterior
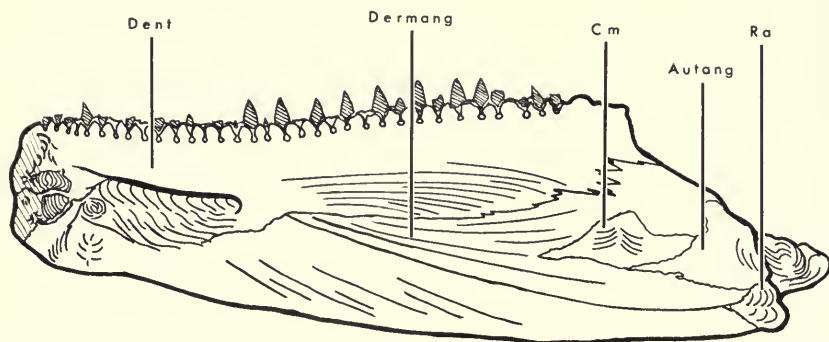
FIG. 6. *Saurodon leanus.* Medial view of right mandible, × 1.5. Based on FM P 27413.

border of the hyomandibular served as the point of attachment for the operculum.

The metapterygoid is a triangular bone joining hyomandibular posteriorly and dorsally, quadrate ventrally, symplectic posteriorly, and mesopterygoid anteriorly. The dorsal half of the metapterygoid is arched medially toward the parasphenoid. Metapterygoid and perhaps also the mesopterygoid were in contact with the basipterygoid process of the parasphenoid, but the structure in this region is unclear. The ectopterygoid is a boomerang-shaped bone with short, stout arms and a dorsoventrally broadened ventral portion. None of the pterygoids show any palatine teeth.

The palatine has a characteristically enlarged anterior head which abuts dorsally against the parethmoid and ventrally articulates with the posterodorsal facet of the maxillary. The lateral surface of this palatine head is convex rather than deeply concave as in *Saurocephalus*. The parethmoid articular facet of the palatine occupies the broad central region of the palatine head and is almost equal in length to the ventral facet for the maxillary.

The triangular quadrate joins the ectopterygoid anteriorly, metapterygoid and mesopterygoid dorsally and articulates with the mandible ventrally. The convex condyle for articulation of the mandible is twisted anteriad to the dorso-ventral axis of the quadrate thus creating an upward slant to the mouth. Posterodorsally the quadrate is cleft for the flattened, triangular symplectic. About half the length of the latter bone is inserted into the quadrate. The broader, dorsal portion extends above the quadrate posterior to the metapterygoid and articulates with the hyomandibular.

CIRCUMORBITALS. On the few heads which are preserved intact, one notes the absence of infra- and postorbitals. Apparently, the cheek region was not covered by bone or such bones were easily lost. The supraorbitals, however, are thick bones. The posterior supraorbital is a broad, thick bone attached to the frontal above the anterodorsal corner of the orbit and extending downward over the upper part of the parethmoid. The anterior supraorbital is an elongate, triangular bone lying lateral to the parethmoid and attached dorsally to posterior supraorbital. A pair of short, ovoid nasal bones probably were present but their dimensions are uncertain and they are not shown on the illustration (Fig.5). Some thin, plate-like bone behind the anterior supraorbital may be part of an anterior supramaxillary or a lacrymal (infraorbital).

OPERCULARS. The preoperculum is a crescent-shaped bone, thickened along its anterior border. Posteriorly, this bone becomes thin with an irregular outline. The operculum is a D-shaped bone not significantly ornamented. Interopercular and subopercular have not been seen.

VERTEBRAE. One specimen (FM PF 3741) includes an entire vertebral column of between 99–101 centra. The division between abdominal and caudal centra cannot be determined. Centra are biconcave except for the first which is flattened anteriorly. Centra are approximately round with the ventral surface slightly flattened.

With the exception of the first 3–4 and last 4–5 centra, all show a single longitudinal lateral ridge separating an upper and lower longitudinal groove. Dorsally, each centrum shows a pair of elongate grooves in which the bases of neural arches were situated. The bases of these arches are of thick bone but pass rapidly into thin, anteroposteriorly expanded laminae. A pair of pits for hemal arches is developed on the ventral surface of caudal and perhaps posterior abdominal centra.

The caudal skeleton (Fig. 7A and B) is similar to that of *Ichthyodectes* (Cavender, 1966, Fig. 1). The last ten centra taper gradually in width and height and the last 3–4 preural centra are bent slightly dorsad. The upward arch of these centra is more gentle than in *Ichthyodectes*. The first ural centrum is about two-thirds the size of the first preural centrum. The second ural centrum is an elongate, laterally flattened spike which subtends the third to fifth hypurals. Neural and hemal arches are tightly attached to the centra. Spines arising from these arches are directed sharply posteriad and closely appressed. The short hemal spines become stouter posteriorly; the
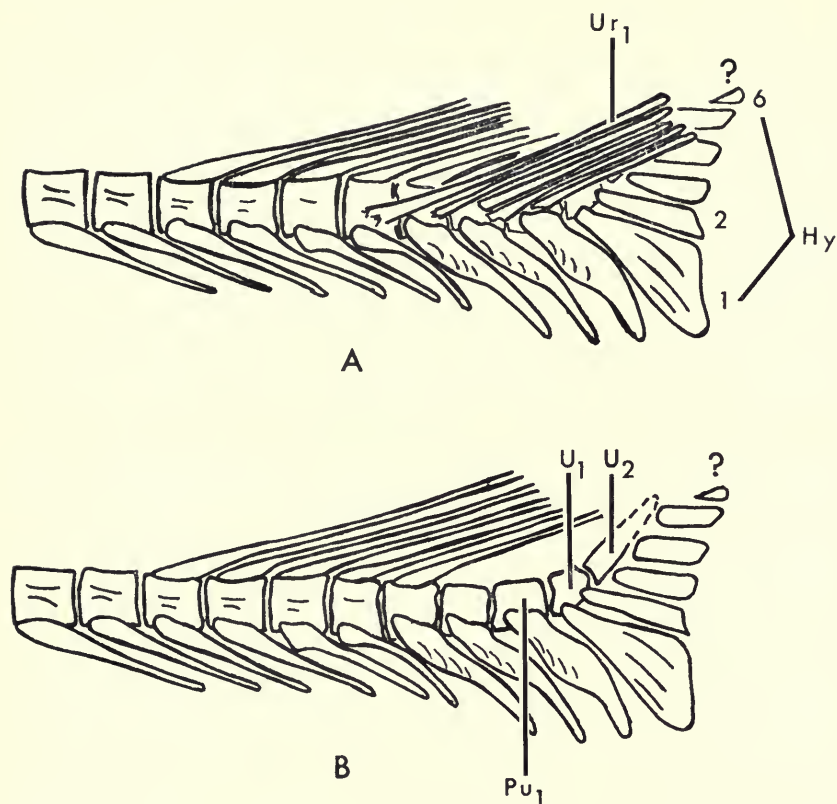
FIG. 7. *Saurodon leanus* Hays. A, Lateral view of caudal skeleton, × 1.0
B, Lateral view of caudal skeleton with urodermals removed, × 1.0. Based on
FM PF 3741.

last three turn sharply ventrad. Spines of the last 4–5 arches are
most intimately involved in support of the caudal fin. Five slender,
elongate urodermals splay-out over and attach firmly to the lateral
surfaces of the last four preural centra.

Six or seven hypurals are present. The first, the broadest and
longest, arises from a depression in the first ural centrum and ex-
pands posteriorly into a plate-like bone. The distal end of this bone
is poorly preserved and whether a process projects from the postero-
ventral border of this hypural, as in *Ichthyodectes*, is uncertain. The
second hypural has the form of an elongate rectangle and arises from
the posteroventral corner of the first ural centrum. Three more

hypurals (3,4,5), each a progressively shorter rectangle, lie above the second and are attached to the second ural centrum. The sixth and apparently last hypural is the shortest and may not have had an osseous attachment to the second ural centrum. The presence of a seventh hypural is uncertain.

PECTORAL AND PELVIC GIRDLES. These units are poorly represented. Preserved parts of cleithrum, coracoid, and scapula apparently have the same shape as in the smaller ichthyodectids. The post-temporal is a broad, oval, plate-like bone with a stout central prong which extends toward the intercalar.

FINS. None of the unpaired fins are preserved. A pectoral fin (FM PF 3741) includes about eight rays. The first ray, about 15 cm. long, is gently curved, and apparently unsegmented. It resembles the first pectoral fin ray of *Ichthyodectes*. The second ray appears to be segmented at some distance beyond its base.

SCALES. One cycloid scale associated with *Saurodon* jaw material (FH 11332) is ovoid, about 1.2 cm. high and 0.7 cm. long. The posterior half bears scattered punctae; the anterior half perhaps a dozen, short radii which do not reach the scale nucleus. This scale probably came from the head region of the fish and probably differs from midbody scales.

Discussion.—Seven nominal species are included in *Saurodon leanus*. After the description of *S. leanus* from New Jersey in 1830, four species were named in the 1870's and three more in the 1890's. All of these species are from the Niobrara Formation of Kansas. Each has been referred to one or more of the following genera: *Saurocephalus, Saurodon, Daptinus* and *Ichthyodectes.*

Saurocephalus prognathus Cope (1870, type AMNH 1912) is based on an apparently composite collection including a right premaxillary, incomplete maxillary, palatine fragment, vertebrae, and fin rays. Some of the material pertains to ichthyodectids (*Xiphactinus*), other parts to pachyrhizoidontids (*Pachyrhizodus.*) The premaxillary whose form Cope appears to have considered most important for establishing this species has a rhomboidal-rectangular shape similar to that of *Saurodon*. The teeth are somewhat less compressed than those of most saurocephalids but not as round as in *Ichthyodectes*. There are seven to eight alveoli on the dental border which is within the range of *Ichthyodectes* and *Saurodon*. Notches in the medial premaxillary wall extend upward from each alveolus. There are no distinct foramina as in most specimens of *Saurodon leanus*, but *Ichthyodectes ctenodon* does not show such vertically elongated notches

on the medial surface of the premaxillary. The lateral surface of the premaxillary exhibits a series of minute lines of punctae resembling the pattern in *Saurodon* rather than in *Ichthyodectes*. Although the type material does not permit complete characterization of this species, there seems less reason to place it in *Ichthyodectes* as Cope (1872) later did than to include it with *Saurodon leanus*.

Saurocephalus phlebotomus Cope (1870, type AMNH 1906) was established on some vertebrae, incomplete jaws, a palatine, and the anterior end of a neurocranium. None of the material is sufficiently complete or distinctive judging from the parts now in the AMNH collection to warrant specific recognition. This is the species which Cope assigned to his genus *Daptinus* (Cope, 1873) primarily because replacement foramina were represented by notches in the medial alveolar margin rather than complete foramina. These notches are less well developed than in *Saurodon prognathus* and do not show in Cope's figure (1875, pl. 49, fig. 2a). The mandibular symphysis resembles that of *Saurodon leanus*. Many specimens have been referred to *Saurocephalus* (or *Saurodon*) *phlebotomus* including a premaxillary (AMNH 1907) which Cope assigned to this species. This individual clearly shows the foramina as in typical *Saurodon leanus*. The type of *S. phlebotomus* perhaps should not be included in *S. leanus* or even in the genus *Saurodon* if the character of tooth replacement foramina alone is essential. However, all of the specimens referred subsequently to *S. phlebotomus* certainly can be included in *Saurodon*. Cope in 1877 on restudying *S. phlebotomus* which he used as the type species of *Daptinus* decided that the latter genus should be dropped and *D. phlebotomus* included in *Saurodon*.

Saurodon broadheadi (Stewart), type KU 153 (old number 212), comprises a left maxillary, ?predentary and eight to nine centra. Stewart did not really compare this material with other species of *Saurodon* except to note the lack of a notch on the medial side of the posterior maxillary condyle which seemed to differentiate it from *S. phlebotomus*. Examination of many *Saurodon* maxillaries shows that notch development is extremely variable, as Stewart himself had shown for the closely related ichthyodectids. The predentary, which according to Stewart was found on the same slab as the maxillary, is incomplete but more suggestive of *Saurocephalus* than *Saurodon* in its relatively short length in comparison to height and the raised posterior facets. However, association of maxillary and predentary was questioned by Stewart so that we may ignore this
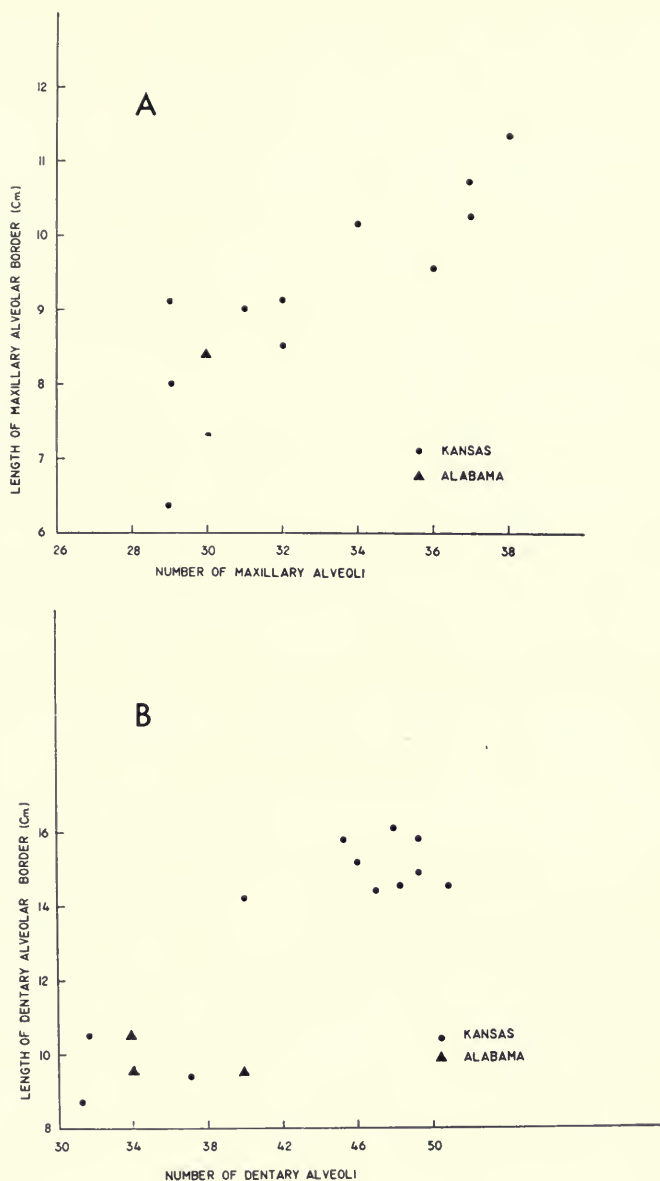
Fig. 8. *Saurodon leanus* Hays. A, Relationship between number of maxillary alveoli and length of maxillary alveolar border. B, Relationship between number of dentary alveoli and length of dentary alveolar border.

apparent generic conflict. Maxillary shape and tooth replacement foramina clearly place this species in *Saurodon leanus.*

Saurodon xiphirostris Stewart (type KU 161) is based on a complete head. Stewart distinguished this species by its elongate slender shape especially in the mandible and predentary. Other specimens (FH 1990, KU 180) show maxillaries, mandibles, and predentaries as long or longer than on the type of *S. xiphirostris.* Proportions of the *S. xiphirostris* maxillary are similar to those of other specimens of *Saurodon leanus.* In the character of number of maxillary alveoli which Stewart cites to differentiate species of *Saurodon*, the type of S. *xiphirostris* falls midway within the range of variation of this character in relation to maxillary alveolar border length. Variation in this character is approximately linear (Fig. 8A). Similar variation can be demonstrated in mandibular and predentary proportions, but data for these elements are less complete. The type of *S. xiphirostris* falls within the linear pattern of variation of mandibular height to length, predentary height to length, etc., characteristic of the suite of *Saurodon leanus* material.

Saurodon ferox Stewart (1898b) is represented by jaws, a predentary, hyomandibular, and palatine. This species was established upon a specimen loaned to Stewart which is not now in a museum collection. Stewart recognized the close similarity between *S. ferox* and *S. xiphirostris.* The small differences in maxillary length, condylar outlines, and number of premaxillary and maxillary alveoli are insignificant for specific distinction. *Saurodon ferox* is essentially like *S. xiphirostris* but with a longer maxillary alveolar border (11.5–8.2 cm.), and more teeth (about 40 to 31). Hay was puzzled by the variation in number of teeth in the three tooth bearing elements of the species named by Stewart. As Figure 8A shows there is an essentially linear relationship between number of alveoli and maxillary length such that recognition of species differences on these characters is unwarranted. Data on relationships of numbers of alveoli to length of the dentary alveolar border (Fig. 8B) are less complete but probably would be similar to those of the maxillary. Relationships between numbers of premaxillary alveoli and premaxillary alveolar border length are similar to those of the maxillary.

Ichthyodectes goodeanus Cope (type AMNH 2110) was assigned to *Saurocephalus* by Hay in 1903. We retain the distinction between *Saurocephalus* and *Saurodon* which Hay did not. The specimen, an upper jaw, palatine, and supramaxillary came from an aberrant individual. The bone is thicker than in other specimens of *Saurodon*

leanus of similar size.   Viewed medially, many replacement teeth are visible in their foramina, unlike the situation in normal *Saurodon leanus*.   These foramina are of irregular size and dispositon above the alveolar margin.   These features suggest that this specimen is a damaged or diseased individual; no other fragment or complete upper jaw resembles this bone in these features.   Nonetheless, shape of the jaw, teeth, type of tooth replacement, and form of the palatine demonstrate that this individual belongs within *Saurodon leanus*.

Saurodon intermedius Newton (1878) is the sole species of *Saurodon* from the English Chalk.   The single specimen, perhaps the only specimen of this genus from the English Chalk, is not unlike *Saurodon leanus* from the Kansas chalk.   It probably comes from the mid-Cenomanian and hence a level lower than the North American fossils.   There are only five premaxillary alveoli compared to a minimum of seven to eight in *Saurodon leanus*.   The 32 maxillary alveoli place *S. intermedius* midway in the range of *S. leanus*.   Other characters such as proportions of maxillary and mandible are similar to those of *S. leanus*.   *Saurodon intermedius* could be referred to *S. leanus* but for reasons of its geographic location, specific distinction is retained.

SPECIES FORMERLY CONSIDERED SAUROCEPHALIDS

In the early 19th century several species based upon isolated teeth were assigned to the genera *Saurocephalus* or *Saurodon*.   Many of the species so named were later transferred to other taxonomic groups.   These species and their suggested affinities are listed below. The authors have not examined any of these species.

Saurocephalus albensis Pictet and *S. inflexus* Pictet were transferred to *Protosphyraena albensis* and *P. inflexa* by Sauvage (1879).   Both species are from the Lower Cretaceous of St. Croix, Switzerland. This assignment must be considered tentative because all other *Protosphyraena* species are from the Upper Cretaceous.

Saurocephalus ferox Gervais was transferred to *Protosphyraena* by Leidy (1857).   This species is also from the Lower Cretaceous.

Saurocephalus picteti Arnaud is a 4 cm. long tooth from the Aptian of Vaucluse, France.   This tooth is too large to be *Saurocephalus*.

Saurodon affinis Kiprijanov, *Saurocephalus lanciformis*, and *S. striata* were named for specimens from the Neocomian of Kursk, Russia

(Kipriajanov, 1860). The teeth are similar to *Protosphyraena* but some of the vertebrae that he illustrated appear to pertain to *Pachyrhizodus*.

Saurocephalus striatus Agassiz, from the Upper Cretaceous of England, was transferred to *Apateodus* by Woodward (1901).

Saurocephalus? lycodon Kner and *Solenodon neocomiensis* Kramberger, the latter a name based on Kner's type, were placed (Woodward, 1901) in synonymy with *Enchodus*.

Saurocephalus marginatus Geinitz pertains to *Cimolichthys* according to Woodward (1901).

Saurocephalus fajumensis Dames, based on teeth from the Lower Tertiary of Birket-el-Qurun, Fayum, Egypt, were transferred to *Sphyraena fajumensis* by Arambourg (1952).

Saurodon conoideus Schafhäutl from the Eocene of Bavaria is a conical tooth perhaps referable to a scombrid.

Saurocephalus inaequalis Münster and *S. substriatus* from the Tertiary are nomina nuda.

Saurocephalus monasteri Münster from the Jurassic is probably a megalosaurian according to Woodward (1901).

Saurocephalus? dispar Hebert teeth from the Cretaceous of Meudon, France, are mosasaurian (Leriche, 1906). Additional teeth described by Geinitz (1868) from Saxony may also pertain to a mosasaur. Likewise supposed *Saurocephalus lanciformis* teeth from the same area (Geinitz, 1875) are probably reptilian.

Saurodon pygmaeus Loomis was transferred to *Ichthyodectes ctenodon* by Bardack (1965).

FUNCTION OF THE PREDENTARY

Saurocephalids are distinguished from other teleosteans by the large predentary which, along with part of the mandible, extends beyond the anterior end of the upper jaw. The triangular predentary commonly is found associated with the mandibles but occasionally as an isolated element. The presence in the saurocephalids of this bone which is not a part of the type material of either *Saurocephalus lanciformis* or *Saurodon leanus* was first recognized toward the end of the 19th century. Premandibular structures are not

unique to saurocephalids and are present in other actinopterygians and one elasmobranch.   None of these fishes, however, is closely related to saurocephalids.

Scombroid fishes of the family Istiophoridae have a denticle-covered predentary (Fierstine and Applegate, 1968).   In these fishes the upper jaw extends anteriorly beyond the end of the lower jaw.   In profile the predentary is triangular but relatively broader transversely than in saurocephalids.   The posterior face is concave and envelopes the conjoined mandibular rami.   Apparently, no other teleostean has an ossified predentary.   A thin, cartilaginous pre-mandibular structure is developed in the exocoetid *Fodiator*.   This predentary is joined to the mandibles by a bracket-shaped suture. A pair of plate-like projections extend anteriorly from the predentary base.   These extensions are joined midcentrally giving the structure an X-shaped appearance in cross-section.   The entire unit is covered by soft tissues which are continuous with those surrounding the mandible.   The function of this structure is not known.   Species of *Trichiurus* (Trichiuridae) exhibit a medially thickened rhomboidal, cartilaginous disc with a posterior prong which is inserted between both mandibular rami.   This structure would function as a pivot on which anterior ends of the elongate mandibles could rotate when the orobranchial chamber was expanded laterally.   A similar struc-ture occurs in *Paralepis*.

The holosteans, *Belonostomus* and *Aspidorhynchus*, have a pre-dentary which does not project beyond the upper jaw.   Mandibular rami of these fishes meet in a thin, elongate suture which runs ventroanteriorly across the long axis of the mandibles and the pre-dentary articulates with the dorsal surface of this symphysis.   A medial and lateral row of teeth are found on the predentary of these holosteans.   Zangerl (1966) described a premandibular element in the Pennsylvanian shark *Ornithoprion*.   This unpaired structure pro-jects beyond the upper jaw and articulates with the paired Meckel's cartilages below the elongated snout.   Teeth are present on this structure.   Zangerl believed that this element was derived from fused anterior ends of Meckel's cartilage.

In saurocephalids, premandibular elements are formed in front of the anterior end of Meckel's cartilage and are of dermal rather than endochondral origin.   In these fishes, the predentary must represent a neomorph derived probably from a separate ossification center of the dentary.   It is difficult to discern places of muscle attachment on teleostean bone and in the saurocephalids there is

no clear evidence of muscle insertions on the predentary. The presence of articular facets at the articulation between mandibles and predentary suggests the possibility that the predentary could move on its articulation with the dentaries. But the only source of a muscle to control such movement would seem to be from the geniohyoid, a slip of which might grow anteriorly across the ventral border of the mandibular symphysis and become attached to the dentary. There would seem to be greater difficulty, though, deriving musculature or ligamentous connections between dentaries and predentary than developing a bony neomorph alone. Thus the predentary probably could not move independently of mandibular motion.

Discussion of the role played by the saurocephalid predentary in locomotory and feeding behavior of these fishes must be speculative in the absence of a structurally similar predentary in living teleosteans. Stewart (1900), who was the first to describe saurocephalid predentaries, assumed that this was a weapon of offense. His vague and, we believe, implausible suggestion perhaps implies its use in a manner analogous to the bill of swordfishes or sawfishes. But in saurocephalids, it is the lower jaw which is elongated. More importantly, the separate premandibular element is articulated to the mandible and in the absence of firm ligamentous or muscular stabilization, the predentary would be vulnerable to dislocation if subjected to lateral stresses similar to those which are applied to sawfish or swordfish rostra. Possibly, the presence of the predentary is related to the structure of the mandibles. Fierstine and Applegate (1968) suggest that the istiophorid predentary developed in order to strengthen the thin symphysial region of the dentaries. A stout predentary would functionally displace the symphysis posteriorly. This would serve to reduce strain on the thin anterior ends of the dentaries as they rotate laterally during expansion of the orobranchial chamber.

Can this explanation of predentary function be applied to the saurocephalids? In contrast to istiophorids, saurocephalid jaws are are dorsoventrally deeper, thicker and shorter. The symphysis is heavy and rugose, reaching its maximum development with the interdigitating structure of *Saurocephalus*. Deep medial pits are found on the dentary where the intermandibularis muscle is inserted. The robust, firmly anchored intermandibularis would serve to limit lateral mandibular movement as well as to adduct the mandibles. With such symphysial modifications there would seem slight need

for a predentary to strengthen the symphysis. Another teleostean, the characin *Hydrocyon*, has an interdigitating symphysial suture and lacks a predentary. Nevertheless, in saurocephalids, the well-developed articulation between dentaries and predentary implies some degree of movement at this point. Facets similar to those of the dentary and predentary are found at the articulation between the palatine and posterior condyle of the maxillary. Here the palatine condyle forms a pivot around which the maxillary turns during opening of the mouth. A slight lateral movement of the maxillary also takes place on this pivot as the posterior end of the maxillary which is joined by ligaments to the dentary moves laterally. Comparable movements, primarily in a lateral direction, must occur between predentary and mandibles. Thus, the saurocephalid predentary could operate in a manner similar to the predentary of the istiophorids. This may not have been the only function of this structure.

A second role of the predentary is suggested by the probable feeding behavior of the saurocephalids. These elongate, slender fishes were no doubt capable of moderate or even rapid speeds for short periods. The slight upward direction of the mouth cleft and the elongate lower jaw projecting beyond the upper suggest surface feeding or at least feeding from below potential prey as in fishes of analogous form today, for example, hemirhamphids. Although no stomach contents of saurocephalids are known, a variety of fish, young reptiles, perhaps Cretaceous birds such as *Ichthyornis*, and even pelagic invertebrates might be engulfed by saurocephalids. The more elongate the lower jaw the greater the area for receiving or stunning prey. If saurocephalids fed by lunging at their prey, as do the hemirhamphids, sudden forward movement by a blunt snouted fish might create turbulence, disturb the flow of water around the fish and perhaps alert the prey. A pointed predentary would maintain a laminar flow of water around the fish.

RELATIONSHIPS OF THE SAUROCEPHALIDS

Determination of the immediate affinities of the saurocephalids presents little difficulty. They closely resemble their Cretaceous contemporaries the ichthyodectids in the suite of characters listed in Table 3. While the relationship between saurocephalids and ichthyodectids is clear, no common ancestor is known. Members of

TABLE 3.   Characters common to saurocephalids and ichthyodectids.

Cranial
General shape of bones and positions of sutures
Large supraoccipital crest
Parietoepiotic ridge
Hyomandibular fossa extending posteriorly onto large intercalar
Post-temporal fossa
Subtemporal fossa
Lateral temporal fossa
General arrangement and size of foramina on postorbital wall
Canal for lateral head vein formed within exoccipital
Palatine enlarged anteriorly forming a malleolar process for articulation between maxillary and parethmoid
Shape, position and relative sizes of mandibular elements

Postcranial
Vertebrae with single mid-lateral longitudinal ridge between two longitudinal grooves
Form of caudal skeleton including two ural centra and five urodermals
Pectoral fin with broad, blade-like first ray

each group easily can be assigned to the Saurocephalidae or Ichthyodectidae. The characteristic features of the saurocephalids, especially the premandibular bone and the method of tooth replacement are not suggested by any ichthyodectid including those known from the Lower Cretaceous.

In recent years the relationships of these families to other teleosteans have been discussed in several papers (Bardack, 1965; Cavender, 1966; Greenwood *et al.*, 1966) but there is no consensus as to their broader affinities. Generally grouped with the clupeiforms, Greenwood et al. suggested that ichthyodectids represent an early offshoot of the osteoglossomorph line of teleostean evolution. Bardack examined the relationships among a diverse group of teleosteans seeking evidence for the existence of a single family (Chirocentridae: Clupeiformes) during the long geologic history of teleostean fishes. These fishes had earlier been placed in several different groups among them leptolepids, chirocentrids, and ichthyodectids. In the discussion presented in that paper distinction of the latter group was recognized informally. Although the Greenwood classification primarily concerns living teleosts, can the ichthyodectids and saurocephalids, as well as several other teleostean groups confined to the Cretaceous, be assigned to the major divisions used in that classification?

The family Ichthyodectidae includes the genera *Chirocentrites, Cladocyclus, Gillicus, Ichthyodectes, Prymnetes, Spathodactylus,* and *Xiphactinus.* This family has representatives from the earliest Lower

Cretaceous (*Spathodactylus*), the uppermost Lower Cretaceous (*Xiphactinus gaultinus, Gillicus serridens, Ichthyodectes minor*), and several horizons in the Upper Cretaceous. Ichthyodectids are known from Europe, North America, Australia and South America.

Greenwood *et al.* distinguish three divisions of teleostean fishes. Contingent upon the evaluation of ichthyodectid and saurocephalid characters, these families may be placed in one or the other of two divisions, namely Division I which includes the Superorders Elopomorpha and Clupeomorpha or Division II which comprises the Superorder Osteoglossomorpha. These authors suggest that ichthyodectids are early derivatives of the osteoglossoid line based on the following characters common to osteoglossids and ichthyodectids: (1) basipterygoid process on parasphenoid, (2) "dentition," (3) subtemporal fossa as in *Osteoglossum*, (4) medially united parietals.

A basipterygoid process is present only in the osteoglossoids among living fishes. However, it occurs in saurocephalids, ichthyodectids whose neurocranial structure is known, as well as leptolepids and pholidophorids. The latter two families are holosteans (or teleosteans depending on the classification followed) ancestral to the teleosts. The basipterygoid process, clearly a primitive teleostean character, is absent from the Clupeomorph(?) *Chirocentrus*, but a transversely concave notch is present on the dorsomedial edge of the metapterygoid lateral to the position from which such a process would arise. This suggests that *Chirocentrus* ancestors also possessed such a process which thus may have had a more widespread distribution than is now realized.

Greenwood refers to the similarity in dentition between osteoglossids and ichthyodectids (1966, p. 360). Osteoglossid dentition includes conical or compressed, medially curved marginal teeth with slightly swollen bases as well as multiple rows on palate, parasphenoid, vomer and copula. Ichthyodectids lack parasphenoid, vomerine, palatal and copula teeth. Teeth of the jaw margins are straight, large and not expanded at their bases. Ichthyodectid and saurocephalid teeth are anchored in deep alveoli rather than ankylosed to the margins of a longitudinal groove as in osteoglossids.

The presence of a subtemporal fossa is a primitive teleostean feature found in their holostean ancestors as well as elopoids. A similar subtemporal fossa appears in the carp. The fourth character, medially united parietals, is again a feature of early teleosteans, such as many elopomorphs as well as the holosteans.

Greenwood *et al.* (1966) distinguish Division II by two primary structures common to all osteoglossomorphs and a group of secondary features restricted to certain orders or families within the division. The former include: (1) Parasphenoid-glossohyal, basihyal bite; and (2) paired, usually ossified rods attached to the base of the second gill arch. In regard to character (1), ichthyodectids and saurocephalids have a narrow rather than broad parasphenoid as in the osteoglossoids and lack parasphenoid teeth. However, the parasphenoid-glossohyal bite is also characteristic of the elopomorphs (Division I) and hence is a primitive teleostean feature. Information on the second structure is not presently determinable from the fossils. The absence of a supramaxillary is also characteristic of the osteoglossomorphs. There are two supramaxillaries in ichthyodectids and at least one in saurocephalids.

Ichthyodectids, saurocephalids, and osteoglossids share several characters in addition to the four discussed above:

(1) Firm union of premaxillary and maxillary. [In osteoglossids the maxillary overlaps the premaxillary, while in ichthyodectids and saurocephalids the premaxillary is attached to a broad lateral depression on the maxillary];

(2) Presence of an orbitosphenoid as in most osteoglossids. [This bone also appears in fishes of Division I];

(3) Presence of a post-temporal fossa;

(4) No auditory fenestra;

(5) No lateral cranial foramen;

(6) Absence of lower intermuscular bones.

In addition to these resemblances, several of which apply to a broad range of early teleosteans, Greenwood *et al.* note other features which they believe are associated with a primary osteoglossomorph character, the parasphenoid-tongue bite. These include:

(1) No process on the maxillary for articulation with the palatine;

(2) Palatine ending anteriorly in a point;

(3) Articulation between parasphenoid and entopterygoid;

(4) Maxillary overlapping premaxillary;

(5) Premaxillary firmly bound to skull.

None of these is characteristic of ichthyodectids or saurocephalids. Additional specializations which distinguish the osteoglossid line from the ichthyodectids include: (1) distinctive caudal skeleton; (2) fusion

of ectopterygoid and palatine; (3) reduction of the suboperculum; (4) circumorbitals usually well developed; and (5) coarse ornamentation of dermal bones and scales.   In contrast to ichthyodectids and saurocephalids, osteoglossids, including the Eocene *Phareodus*, are exclusively freshwater fishes. Another Eocene fish, *Brychaetus*, which may or may not be an osteoglossid, is possibly an inhabitant of marine waters.

Ichthyodectids and saurocephalids have usually been referred to the Clupeiformes based on similarities of the fossils to the living genera *Chirocentrus* and *Megalops*.   These fishes of divergent morphology are included in two superorders of Division I.   Ichthyodectids and saurocephalids show certain characters also developed in Superorder Elopomorpha of Division I.   These include: (1) posttemporal fossa, (2) subtemporal fossa, and (3) conjoined parietals. But the two fossil families differ from extant elopomorphs in (1) absence of a gular plate, (2) hypurals attached to two rather than three or more centra, and (3) no bone enclosed ethmoidal commisure.

Considering resemblances and differences between the two families of fossil fishes and the living fishes of Divisions I and II, what should be the taxonomic assignment of the Ichthyodectidae and Saurocephalidae?   Divisions I and II include fishes whose ancestry is near or at the holostean level.   However, several of the characters distinguishing these divisions make it difficult to include the two families concerned.   Thus, fishes of Division I have a high coronoid process on the mandible, parasphenoid and pterygoid teeth, a full complement of intermuscular bones, and an ethmoidal commissure for the sensory canal.   Fishes of Division II show the tendency for fusion of the premaxillaries into a single bone, teeth on the parasphenoid, glossohyal and pterygoids, fusion of palatoquadrate arch elements, reduction of foramina for components of the fifth and seventh nerves and associated blood vessels, a distinctively modified caudal skeleton, and reduction of the suboperculum.

Mesozoic teleosts lacking Tertiary descendants may be placed in extant taxa which results in increasing difficulty of circumscribing and defining these taxa.   Or, they may be separated as distinct groups albeit with the recognition, not taxonomically expressible, that they exhibit many features similar to or later developed by surviving lineages.   Cretaceous teleosts are becoming better known. New genera are being described and several Tertiary or even living forms may be traced back to the Cretaceous.   Yet some of the dominant (in terms of numbers of specimens and their geographic distri-

bution) types remain unique to the Cretaceous. A similar pattern is seen in other groups of vertebrates during certain periods of their evolutionary history especially when the group is undergoing relatively rapid diversification. This diversification is emphasized by distinguishing taxonomically at least those groups which represent blind ends of the radiation. Such is the case with the Ichthyodectidae and Saurocephalidae. Therefore it is suggested that these fishes be separated as a distinct order defined as follows:

Order Ichthyodectiformes: Elongate slender fishes. Supraoccipital crest large, parietals united midsagittally. Deep post-temporal and subtemporal fossae. Hyomandibular fossa extending onto intercalar. Broad articulation between parethmoid and palatine. Premaxillary firmly united to lateral face of maxillary. Single row of teeth in deep alveoli on premaxillary, maxillary and dentary. Vertebrae with lateral, longitudinal ridge. Two ural centra. Pectoral fin with broad, blade-like first ray.

Recognizing ordinal distinction for these families still leaves the question of the relationship of this order to other teleosteans. Clearly ichthyodectiforms have several characters which are also developed in elopomorphs and osteoglossomorphs. Other groups of Cretaceous teleosteans also show a mosaic of elopomorph and osteoglossomorph characters. Pachyrhizodontids show a post-temporal fossa, a single row of teeth with swollen bases on the lateral jaw margins, and no mandibular coronoid process. Apsopelicids exhibit post-temporal and subtemporal fossae, and a mandibular coronoid process. Fishes of both of these families lack a gular plate, ethmoidal commissure, and parasphenoid teeth. These families and others are part of an increasingly broad Cretaceous teleostean complex. The extension of Divisions I and II from the recent back into the Cretaceous would create artificial separations among fossil groups. During the Cretaceous multiple evolutionary lines of teleosteans developed from several holosteans and still unknown teleosteans. Broad, but still inchoate divisions of Late Mesozoic teleostean history are emerging and they indicate a greater diversification of these teleosts than is evident from the living forms.

ABBREVIATIONS FOR FIGURES

amc.—vomerine facet for anterior condyle of maxillary
Autang.—autangular
Boc.—basioccipital
Cm.—coronomeckelian
Dermang.—dermangular
Dent.—dentary
d. oss. br.—depression for osseous brushes
eff. ps. a.—foramen for efferent pseudobranchial artery
epl.—ethmoid facet for ethmoid-premaxillary ligament
Epot.—epiotic
Eth.—ethmoid
Exo.—exoccipital
f. hym. VII—foramen for hyomandibular branch of seventh nerve
f. m.—foramen magnum
Fr.—frontal
Hy.—hypural
hym. f.—hyomandibular fossa
Int.—intercalar
int. car. a.—foramen for internal carotid artery
lat. head v.—lateral head vein
lat. temp. f.—lateral temporal fossa
o. a.—foramen for orbital artery
occ. n.—occipital nerve
Ors.—orbitosphenoid
ot. VII.—foramen for otic branch of seventh nerve
pal.—parethmoid facet for palatine malleolus
Par.—parietal
Pareth.—parethmoid
Pas.—parasphenoid
p. pal. VII.—foramen for posterior palatine branch of seventh nerve
Pro.—prootic
pro. br.—prootic bridge
ptm. f.—post-temporal fossa
Pto.—pterotic
Pu_1.—preural centrum$_1$
Ra.—retroarticular
se. f.—subepiotic fossa
Soc.—supraoccipital
Sph.—sphenotic
stm. f.—subtemporal fossa
$U_{1,2}$ —ural centrum$_{1,2}$
Ur_1—urodermal$_1$
Vo.—vomer
X.—foramen for vagus nerve

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